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On multifaceted definitions of multilevel societies: Response to *Papageorgiou and Farine*

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Papageorgiou and Farine [1], in their comment on our recent synthesis of animal multilevel societies [2], provide several examples of nestedness in avian social systems and call for a fuller incorporation of birds into our theoretical framework. We focused mainly on mammals to construct our proposed framework because multilevel societies are best known from this taxonomic group. Papageorgiou and Farine [1] point out several bird species that form nested social arrangements and argue that, by diving deeply into examples from birds, there may be variations in form that meet our criteria for a multilevel society—a social system with a stable core level and at least one recognizable upper level. Papageorgiou and Farine [1] raise two questions: first, whether the operational definition of multilevel societies should be relaxed to accommodate bird species that show more stability at higher levels of society; and second, whether societies with multiple tiers resulting solely from habitat preferences instead of social preferences should be classified as multilevel societies.

With regard to the first question, Papageorgiou and Farine [1] argue that our criteria should be relaxed to include social stability at any level of a nested society and that the core unit does not necessarily need to be the lowest level. However, we maintain that (i) encompassing every society with a demonstrable modular structure would invalidate the inclusion criteria we developed for distinguishing multilevel societies from other types of systems with detectable substructure; and (ii) a more permissive definition would hamper efforts in identifying the eco-evolutionary drivers of multilevel societies *sensu stricto*. Moreover, maintaining this distinction between multilevel societies with at least two consistent levels and societies with a single stable level combined with other unstable associations (as seen in several bird taxa) is crucial because evolutionary processes such as information flow and disease transmission are expected to differ between these types of societies. That said, we are not opposed to the idea that the most stable levels can be higher levels rather than the core unit. Societies with stable intermediate and upper levels, yet unstable lower levels (as exemplified by vulturine guineafowl *Acryllium vulturinum*; [3]), could constitute multilevel societies, as we originally acknowledged [2]. In fact, in our discussion of the multilevel alliance system of the Shark Bay bottlenose dolphins (*Tursiops* sp.) we pointed out that this system deviates from our definition in that the highly cohesive and stable units (second-order alliances) occur at a level above the core unit. According to our framework, however, a society with unstable core units, no intermediate level, and clearest membership at a higher level would not represent a multilevel society but instead a system with atomistic fission-fusion dynamics. This is exemplified by the northern muriqui (*Brachyteles hypoxanthus*), which exhibits flexible association patterns at basal levels but cohesiveness at the upper level, both spatially and temporally [4].

Papageorgiou and Farine [1] shortlist five possible avian candidates for multilevel societies. But which ones do actually fit our definition? Beyond vulturine guineafowls, bell miners (*Manorina melanophrys*) may be a good fit, as discrete social organization manifests itself on at least three levels [5]. Two additional species appear to 'tick the boxes'. In spectacled parrotlets (*Forpus conspicillatus*), monogamous pairs are embedded within putatively stable groups which then form flocks [6]. This does appear to be a multilevel society, but more data on association patterns are probably needed to rule out alternatives. In white-fronted bee-eaters (*Merops bullockoides*), there is an intermediate social tier between the breeding pair and the larger colony [7], which could qualify their society as multilevel. Careful screening of the literature will likely reveal similar systems in hitherto neglected taxa.

The second major question raised by Papageorgiou and Farine [1] pertains to whether the definition of multilevel societies should include structured societies brought about by shared spatial preferences or other ecological opportunities (e.g., preferences for certain sleeping and foraging sites) instead of social preferences. In some cases it is not known to what degree the formation of a distinct level is ecologically induced or the result of individual expressions of social preference. For some species, we still do not know exactly where the social glue ends and habitat-induced overlap begins, i.e. at which spatial scales the social processes are paramount. While core (and intermediate) levels are undoubtedly genuine social groupings that crystallize for reproductive purposes and social support, we should be open to the idea that assortment into upper-level groupings is not exclusively driven by social preferences but may also involve ecologically driven mechanisms. Apex levels in particular often represent aggregations of individuals resulting entirely from an external factor, e.g. the magnetic effects that localized resources exert on social units, as is the case with rare safe sleeping sites in the classic example of the troop level in hamadryas baboons [8]) which are very different from a 'group' of individuals in which the presence and identify of conspecifics matter. Lack of individualization, however, does not preclude the possibility that individuals derive benefits from being associated with the apex grouping level (e.g. 'safety in numbers').

Because we cannot always ascertain whether a particular level of a multilevel society is socially or ecologically driven, this should not be a decisive factor in classifying a society as multilevel or not. In our view, the critical criteria are (1) consistency of individual membership in each level over time and (2) spatio-temporal cohesion of the core and upper levels. An important goal for future research is to quantify the relative contributions of social processes and ecological factors in shaping additional levels in animal societies. This will require fine-grained data on how animals

move relative to each other, and, ideally, on how they may perceive each other as individuals and members of distinct social levels. It would also be interesting to compare the consistency of groupings that are purportedly socially versus ecologically driven. Papageorgiou and Farine [1] argue that studies from birds can allow social versus non-social drivers of nested social levels to be disentangled. While we agree that a broader perspective is useful, it is not clear to us how birds are in any way more suitable than mammals for distinguishing the drivers of social levels, particularly as few of their examples are unambiguously multilevel. Clearly, much further work is needed, and data from mammals, birds and other taxa will be crucial in enriching and refining our understanding of the evolutionary processes responsible for the emergence and maintenance of this intriguing social system.

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